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Milyutin,
L. I.

Predicting Responses to Climate in Eurasian Populations of *Pinus Sylvestris* and *Larix*

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RUSSIA: V.N. SUKACHEV INSTITUTE OF FOREST,
SIBERIAN BRANCH
FS Contact: Dr. Gerald Rehfeldt
Coop Contacts: Dr. Lenoid Milyutin,
Dr. Nina Kuzmina
Dr. Nadja Tchebakova

Predicting responses to climate in Eurasian populations of *Pinus sylvestris* and *Larix* spp. from disparate series' of provenance tests

L. I . Milyutin, N. A. Kuzmina, N. M. Tchebakova, A. I. Iroshnikov
Sukachev Institute of Forest, Krasnoyarsk, Russia
G. E. Rehfeldt, W. R. Wykoff
Rocky Mountain Research Station, Moscow, USA

INTRODUCTION

A. Genes and climate

B. Ecology and genetics of and *Pinus sylvestris* and three species of *Larix* (*L. sibirica*, *L. gmelini*, and *L. sukaczewii*). Use Abaimov et al, 1998.

Objectives: to develop and interpret climate transfer functions that predict the performance of Eurasian pine and larch populations from the change in climate experienced by populations when they are moved from their provenance to a planting site. Throughout this paper, the term 'provenance' is used to designate a geographic location; 'population' refers to the individuals at that location and their wind-pollinated descendants.

METHODS

The height and survival of provenances of *Larix* spp. and *P. sylvestris* were collated from published provenance tests (Tables 1 and 2), all of which had been established in the latter half of the 20th Century. These tests included a broad spectrum of provenances that covered the species' distribution throughout much of Eurasia. Pine data were available from 313 provenances for the analyses of height and 228 provenances for the analyses of survival; however, of the sites listed in Table 1, survival data were available for only the first eight. For *Larix* spp., heights and survivals were available for 130 provenances, 63 of *L. sibirica*, 35 of *L. gmelinii*, 25 of *L. sukaczewii* and 7 of *L. decidua*. No survival data were available for Bronnitsky-1 and Chita (Table 2).

Provenances of both species, but especially those of the pine, had been planted on a numerous sites that sampled a broad range of climates (Tables 1 and 2). Test sites for the pine, for instance varied in mean annual temperature from 11.9 to -7.0, while those for larch varied from 6.4 to -3.1. For the pine, a subset of provenances had been planted on 39 sites with an average of 44 at each site. For larch, about 30 provenances were represented at each of eight sites.

Because the provenance tests were of disparate series', measurements of height and survival not surprisingly had been made at different ages; 7 to 17 for the pine and 9 to 13 the larches. The latest age at which survival had been scored varied from 7 to 11 in the pine and from 5 to10 in the larchs. Because of these disparate ages of measurement, heights were adjusted for age before being analyzed. For survival, however, the assumption was made that the latest date at which survival was scored reflected climate-induced mortality, with subsequent mortality accumulating largely for reasons other than climate. Therefore, no attempts were made to adjust survivals for age of scoring.

Adjustments of height data for age were made in two steps: (1) develop a regression of height on age and (2) adjust provenance data at each test site according to that regression. For the pine, at only one planting site, Suhobuzimo-1 (Table 1), were measurements available for

multiple ages, 7 and 12. For larch, measurements had been made at ages 4 and 10 at Krasnoyarsk (Table 2), 3 and 11 at Uzhur, and 5 and 12 at Tanzybei. For both species, provenance means from each of these sites were used in a regression from which height could be predicted from age:

$$Y_i = a + bX \qquad [1]$$

where Y is the mean of provenance i , a and b are regression coefficients, and X is the age of measurement. Quadratic regressions were also made but were inferior to the linear and are not presented.

The linear regressions were then used to adjust height measurements for age according to the relationship:

$$Y'_{ijk} = Y_{ijl}\,\hat{Y}k\,\hat{Y}l^{-1} \qquad [2]$$

where Y'_{ijk} is adjusted height for population i at planting site j for standard age k, Y_{ijl} is the observed height at age l, $\hat{Y}k$ is the predicted height for standard age k, and $\hat{Y}l$ is the predicted height for age l. Predicted heights were calculated from linear regression [1]. For larch, the adjusted was the average of the predictions made individually by the three available regressions. The standard age was 11 for the pine and 12 for the larches.

The effectiveness of these adjustments was assessed with independent provenance test data[1]. For pine, height measurements of many of the same provenances was available from 8 planting sites in North America, three in Maine (USA), one in Minnesota (USA), and four in Alberta (Canada). For larch, the effectiveness of the adjustments were tested with data from two sites: Bronnitsky-1 (Table 2) where multiple measurements had been made, and in Alberta where Eurasian species of larch have been introduced. Effectiveness was judged according to the regression of the adjusted height on the observed, and specifically by whether (1) the regression coefficient deviated from a value of 1.0 and (2) the intercept differed from zero.

Five climate variables were considered for relating responses to climate: growing degree-days>5, degree-days<0, annual moisture index (growing degree-days>5/mean annual precipitation), mean annual temperature, and Conrad's (1947) continentally index. These five have been shown to be useful in describing performance according to the distance in climate space that provenances have been transferred to a planting site (Rehfeldt et al, 1999). Normalized climate records (Gidrometeoizdat. 1966-1970) from those stations closest to the provenances and planting sites were use to characterize the climate at each. The independent variables used in the Weibull regression were the difference in climate between the planting site and provenance (planting site climate minus provenance climate). Our analyses thus were based on the distance in climate space that populations were moved from their provenance to a planting site. This distance can be viewed as either a climate transfer distance of a population from its provenance to a test site, or as the amount that the climate of a provenance has changed from that to which a population is adapted.

To calculate the effects of a change in climate on the height and survival of populations, Weibull response functions were fit to adjusted heights and survival with climate transfer

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[1] Unpublished data provided by Drs. C. C. Carter, University of Maine, Orono, Maine; C. A. Mohn, University of Minnesota, Minneapolis, Minnesota; and N. K. Dhir, Alberta Environment Protection, Edmonton, Alberta.

distances as independent variables. The Weibull function was chosen because it can assume the shape of either normal or skewed normal distributions (see Johnson et al., 1994) which intuitively seem appropriate for biological responses to climate. Dr. Run-Peng Wei (Environmental Protection, Alberta Lands, Edmonton Alberta) provided the conversion of the Weibull density function (Johnson et al., 1994) to a Weibull response function from which response Y (height or survival) is predicted from X:

$$Y = c(X'-\delta)^{(\alpha-1)} \exp\left(-\frac{(X'-\delta)^{\alpha}}{\beta}\right), \qquad [3]$$

where

$X' = (X - X_{\min}) / (X_{\max} - X_{\min})$

c = performance capacity, > 0

α = shape parameter, > 1

β = scale parameter, > 0

δ = position parameter, $< X'$

Note that climate transfer distances (X) are transformed such that the transformed X' has a relatively small scale, a positive value, and is greater than δ.

When transformed into a form suitable for non linear regression, [3] becomes:

$$\log Y = \log c + (\alpha-1)\log(X'-\delta) - \frac{(X'-\delta)^{\alpha}}{\beta} \qquad [4]$$

$\Rightarrow$

$$Y' = c' + a_1 \log(X'-\delta) + a_2 (X'-\delta)^{(a_1+1)} \qquad [5]$$

let $X_1' = \log(X'-\delta)$ and $X_2' = (X'-\delta)$

then

$$Y' = c' + a_1 X_1' + a_2 X_2'^{(a_1+1)} \qquad [6]$$

where

$c' = \log c$,

$a_1 = \alpha - 1$ which is < -1

$a_2 = -\frac{1}{\beta}$ which is < 0

Before performing the Weibull analyses, however, two assumptions were invoked concerning ecological responses to climate. Because provenance tests are costly, tests are rarely established in ecologically marginal climates where growth and survival are expected to be poor. For this reason, measures were taken to assure that the resulting Weibull model would be asymptotic to zero for large absolute values of climate transfer. This was done by adding to the climatic data set two dummy observations that were given a value of zero for both height and survival for climates known to be beyond the ecological distribution of the species'. Secondly,

our analyses consider climate responses as univariate effects when, in fact, climate variables interact to determine responses. To incorporate the concept of limiting factors in our analyses, therefore, observations were eliminated from the Weibull analyses if (1) the climate transfer variable (X) was within ± 1/2 standard deviations of zero, (2) the response (Y) was less than the mean, and (3) the value of X for any of the other climate transfer variables was greater than two standard deviations above or below zero. From these procedures, resulting predictions would reflect the fact that high levels of performance under optimal climatic conditions for one variable could not occur when other climatic variables were marginal. The procedures eliminated for the pine between 3% and 7% of the observations and between 1% and 3% for analyses of larch. Screenings were done separately for each of the independent variables.

The Weibull response function was then fit to population heights and survivals for each of five independent variables quantifying the difference in climate between the provenance and test site. For larch, data from *L. decidua* was deleted and Weibull analyses were performed separately for each species. To obtain the coefficients that provided the minimum residual mean square, Weibull response functions were performed iteratively to find a value of $(X'-\delta)$ in [5] that minimized the residual mean square. For pine, Weibull analyses were base on 1570 to 1637 observations for height and 372 to391 for survival; larch analyses for both response variables were based on about 135 observations for *L. sibirica*, 59 for *L. gmelinii*, and 45 for *L. sukaczewii*. The fit of the Weibull response function was judged by correlating predicted values with observed.

The Weibull function produced a response surface that described height and survival according to the change in climate experienced by a populations when it was moved from the provenance to which it is adapted to a foreign climate at a planting site. Predicted responses, therefore, reflected a mean response of all provenances to the climate change. However, at any planting site, responses are influenced by factors other than climate, and these additional factors can be either genetic or environmental. Of the environmental, soils, insects, and diseases, for instance, can strongly influence responses. It is unfortunate, therefore, that without suitable data, these influences must appear as error variances to our models. By contrast, for genetic factors, it is well documented that for forest trees in general and for *P. sylvestris* and *Larix* spp. in particular (Iroshnikov, 1977), populations differ in innate growth potential. These differences, moreover, tend to be controlled through natural selection by the climate of the provenance. Because a negative relationship generally exists intraspecifically between growth potential and tolerance to the cold for populations of forest trees, we expected the residuals from the Weibull regression to be largely negative for populations from relatively cold climates and to be largely positive for populations from relatively warm climates. Therefore, to improve the predictive capabilities of our models, a quadratic function was used to fit provenance climate to residuals from the Weibull function:

$$R_{ij} = a + b_1 X_i + b_2 X_i^2 \qquad [7]$$

where R_{ij} is the residual for population i at test site j; and X_{ik} is the climate variable k at provenance i . The five original climate variables were tested as independent variables for relationships with the residual: growing degree-days>5; degree-days<0, annual moisture index, mean annual temperature, and the continentally index.

These analyses thus produced five quadratic regressions for each of the 10 Weibull models that were available for the pine and larch. Of the five, the one with the lowest residual

mean square was used in combination with the corresponding Weibull model to produce a general response model from which performance in height or survival could be predicted from (1) the distance in climate space that a population was moved from its provenance to a test site and (2) the general climate of the provenance.

Both the Weibull and combined response models were validated were validated with independent data from the same North American trials that were used to assess the effectiveness of our height adjustments. Validations were made for only the models predicting height; no data were available for validating the survival models.

RESULTS

To validate the procedure by which heights were standardized for a common age, regressions of adjusted height were made on predicted heights using independent data (Tables 3 and 4). These analyses allowed the slope of the regression to be compared to an expected value of 1, and the intercept to be compared to an expected value of zero. For the pine, all but two of the eight tests produced regression coefficients that differed significantly from 1.0, three of which were substantially larger (Table 3). Of these three, all but the comparison for Duck Lake produced errors of estimate that were less than 10 % of the mean. The table also shows that the intercepts produced by these regressions differed from zero in three of the eight comparisons. However, judging from the absolute size of the regression coefficients and percent error, only the comparison for Duck Lake badly failed validation. For Duck Lake, moreover, comparisons required extrapolation to age 20 of the Suhobuzimo regression that was based on a maximum age of 12. Consequently, it is not necessarily surprising that validation failed. For larch (Table 4), however, regression coefficients did not differ from 1, intercepts did not differ from zero, and the error was only 4 percent of the mean, thereby providing strong validation of the approach. In total, these analyses suggest that as long as extrapolation is not excessive, the approach can be used to adjust for disparate ages without creating excessive bias.

All of the Weibull regressions were statistically significant. For height analyses of pine, (Table 5), the simple correlations of predicted with observed were all statistically significant ($P < 0.01$). However, of these regressions, the most effective those involving climate transfer in units of the continentally index, negative degree-days, and mean annual temperature. For survival, all regressions except that driven by degree-days>5 were significant ($P < 0.01$), but those driven by negative degree-days and mean annual temperature were the strongest. For the height of larch (Table 6), all regression models were statistically significant, and, as shown by the simple correlation between observed and predicted, all models were effective predictors. For larch survival, however, the model driven by the moisture index was by far the most effective. Figures 1 and 2 illustrate the fit of the Weibull function for height and survival of pine while Figures 3 and 4 illustrate the fit of the same dependent variables for the three species of larch.

A screening of provenance climates for association with the residuals from the Weibull regression showed that for the pine, degree-days >5 accounted for the most variance in the residuals for all models except that predicting survival from the change in mean annual temperature. For this model, provenance moisture index was the most closely related to the size of the residual. When these models were combined with the Weibull function into a general response model, (Figures 5 and 6), simple correlations between the predicted and observed remained statistically for all models (Table 5). Of the general response models, however, that for the pine (Table 5) driven by the change in moisture index seemed to be inferior for predicting

height, and that driven by the change in degree-days<5 was decidedly inferior for predicting survival. Both the Weibull and combined response models predicting height received strong validation with independent data (Table 7) even though Weibull model driven by degree-days>5 itself could not be validated.

Similar screenings for larch showed that the mean annual temperature accounted for the most variance in the residuals for models predicting height, while provenance moisture index explained the most variance in the residuals for survival. The combined response models (Figures 7 and 8), produced simple correlations between the predicted and observed that were statistically significant for all models (Tables 6 and 8). However, for predicting height, the general response models driven by climate transfer in units of mean annual temperature and degree-days>5 seemed the most effective. For predicting survival, the response model driven by change in units of the moisture index was the strongest. Validations (Table 8) of the models predicting height were strongly supportive even though the Weibull model driven by change in units of degree-days>5 could not be validated.

Statistics useful for interpreting the Weibull regression models are presented in Tables 9, 10, and 11. These statistics show, first, the X- and Y-axis coordinates for the apogee (Y_{max}) of each Weibull model. The other statistics pertain to confidence limits about the predicted value at the apogee. Of these limits, the lower intersects with the regression line at two points. As illustrated by Rehfeldt et al. (1999), the X-axis coordinates of these points, X_1 for the smallest value and X_2 for the larger, define the amount that the climate must change before one can be reasonably certain of a statistically significant change in the response (Y). As long as the interval between X_1 and X_2 includes zero, the optimum climate does not differ statistically from a climate change of zero units at a probability equal to that used for the confidence interval about Y_{max}. For our analyses, we use a probability of $\alpha = 0.2$ for the confidence intervals. This relatively high level of probability limits type II errors (accepting no differences when they are real) which produce the most harmful effects when model are applied to practical problems.

Table 9 shows, for instance, that the model describing the height of pine as driven by the change in moisture index, peaks at a change in moisture index of -0.3 where predicted height is expected to be 251 cm. A climate change of $X_1 \leqq -1.08$ or $X_2 \geqq 0.48$ units, moreover, will produce a statistically significantly ($\alpha = 0.2$) decrease in response (Y). However, because the interval between X_1 and X_2 includes zero, the model suggests that the tallest trees will be produced when a population is grown in the climate of its provenance (a change of zero units in moisture index). Bold-face values of the X-axis coordinates of the confidence interval point to those climate variables for which height or survival would be enhanced by a change in climate.

Table 9 shows in general that the growth of pine populations will be enhanced if grown climates slightly warmer than that of their provenance, provided that the moisture index is constant. This means that the climate must not only be warmer but also must be somewhat wetter. Survival, however, is enhanced if populations are grown in climates considerably warmer in the winter with, therefore, a higher mean annual temperature and a much less severely continental climate, provided, again, that the moisture index remains constant.

Interpretation of the Weibull responses for the species of larch (Table 10 and 11) suggest that the optimal climate for height of *L. sukaczewii* populations will occur when grown in the climate of it's own provenance; height is optimized, therefore, with zero units of climate change. For *L. sibirica*, however, height is optimized in climates warmer than that of the provenance as long as the moisture index remains constant. Although none of the confidence intervals for *L.*

gmelinii exclude zero, values of X for Y_{max} tend to be skewed strongly toward warmer climates. Therefore, despite a lack of statistical significance, the conclusion seems sound that the growth of populations of this species would be enhanced by both warming temperatures and increases in the moisture index (more heat per unit moisture). For survival, however, optimal response of all three species would occur when populations are grown climates that are warmer and somewhat wetter with, therefore, a with a higher moisture index than their provenance. This means that optimal performance of *L. gmelinii* should occur in climates typically inhabited by *L. sibirica*; and those of *L. sibirica* on those typically inhabited by *L. sukaczewii*.

The combined response functions are illustrated in Figures 5 and 6 for the height and survival, respectively, of the pine, and in Figures 7 and 8 for height and survival of the three species of larch. While illustrating the statistics of Tables 9-11, these figures also illustrate the importance of taking into account the climate of the provenance in predicting responses. Because differential growth and survival of populations are responses controlled in part by climatic selection, one expects populations from different climates to have different responses. Thus, for pine, when comparing populations growing in or near to the climate to which they are best adapted (climate transfer of zero), populations from warm climates are expected to have the highest predicted heights, but not necessarily the highest survivals. For height, maximal values are expected for populations with about 2000 degree days>5 (Figure 5) while for survival, maximum values occur for populations from 800 degree-days (Figure 6).

Because the three species of larch customarily inhabit different temperature regimes, the combined response models become more complex (Figure 7). In *L. sukaczewii*, which tends to inhabit the warmest climates, populations with the highest growth potential tend to come from climates with mean annual temperatures that are among the coolest (-3°C) inhabited by this species. In *L. sibirica* which inhabits climates intermediate to those occupied by *L. sukaczewii* and *L. gmelinii*, populations from climates with a moderate mean annual temperatures (e. g. -2° C) tend to have the highest growth potential, with populations from sites either warmer (5°C) or colder (-8°C) being inferior. In *L. gmelinii* which inhabits the coldest sites, populations with the highest growth potential tend to come from climates that are among the warmest (mean annual temperature of 0°C) while those from the coldest sites have the lowest.

Survival of populations in the three species of larch tend to follow the same patterns with regard to the moisture index (Figure 8). When comparing populations growing in the climate where they best adapted, highest survival tends to be from populations adapted to climates with relatively high moisture indices (high heat per unit of mean annual precipitation). Survival of populations from climates where degree-days>5 are approximately equal to the mean annual precipitation (moisture index of 1) is expected to be the lowest.

DISCUSSION

A. ecological interpretations
B. practical applications
   1. seed transfer in reforestation
   2. assessment of biological basis of current seed zones of Russia
   3. responses of contemporary pine and larch forests to a change in climate

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Table 1. Location, general climate, and mean annual temperature of *P. sylvestris* planting sites.

planting site	latitude °N	longitude °E	mean annual temperature	age	number of provenances	reference
Suhobuzimo-1	56.50	93.25	-1.3	12	97	a
Suhobuzimo-2	56.50	93.25	-1.3	12	69	a
Uzhur	55.30	89.83	-1.0	10	60	a
Tanzybei	53.17	92.92	-0.8	12	137	a
Boguchany-1	58.42	97.42	-2.5	11	81	a
Yenniseisk	58.48	92.17	-1.9	11	19	b
Zaudinsk-1	51.83	107.67	-2.9	7	59	c
Monchyegorsk	67.85	32.95	-0.7	14	35	d
Plyesyetsk	63.10	40.30	0.8	15	26	d
Chyeryepovyets	59.18	38.00	2.6	15	35	d
Kortkyeros	61.70	50.80	0.4	15	23	d
Chupa	66.37	33.00	0.5	16	16	d
Myedvyezhyegorsk	62.90	34.40	1.5	16	45	d
Lisino	66.20	30.70	0.2	15	41	d
Pskov	57.83	28.43	4.6	15	37	d
Jarva	59.40	25.90	4.2	11	45	d
Lenino	52.40	31.00	6.1	15	41	d
Tsyurupinsk	46.50	32.50	10.4	16	38	d
Izyum	49.00	37.50	7.2	15	42	d
Sambor	49.50	23.20	7.5	11	33	d
Olyevsk	51.23	27.67	6.6	15	37	d
Kovrov	57.20	43.00	2.6	15	87	d
Davydovka	50.90	39.00	6.1	17	83	d
Lunino	53.20	45.00	3.9	17	54	d
Kamyshin	50.17	45.40	6.5	17	31	d
Zyelyenodolsk	55.90	47.50	3.0	17	37	d
Ufa	55.00	56.00	2.8	17	36	d
Kungur	57.40	56.90	1.3	17	31	d
Ryevda	56.83	59.97	0.7	17	32	d
Zvyerinogolovskoy	54.50	64.90	1.0	17	32	d
Buzuluk	52.78	52.25	3.5	17	37	d
Suzun	53.83	82.33	0.0	17	35	d
Boguchany-2	58.42	97.42	-2.5	16	73	d
Turukhansk	65.80	87.88	-7.0	14	17	d
Zaudinsk-2	51.83	107.67	-2.9	16	51	d
Svobodnyl	50.20	128.17	-2.2	7	10	d
Urumkal	52.70	70.00	1.0	9	7	d
Dolon	50.80	80.50	3.1	10	11	d
Shyekinskil	41.22	47.15	11.9	12	33	d

[a] Iroshnikov, 1977, omitting Olrec Rechka (poor survival)
[b] Kuzmina NEED REFERENCE
[c] Cherepin, 1980 NEED REFERENCE
[b] Cherepin, 1999 NEED REFERENCE
[d] Shutyaev and Gierytch, 1997, omitting Kazlu-Ruda (data at age 5)

Table 2. Location, general climate, and mean annual temperature of *Larix* planting sites.

planting site	latitude °N	longitude °E	Mean annual temperature	age	number of provenances	reference
Suhobuzimo	53.30	98.81	-1.3	10	46	[a]
Uzhur	53.63	100.04	-1.0	11	31	[a]
Tanzybei	53.80	101.44	-0.8	12	53	[a]
Bronnitsky-1	56.20	71.94	3.2	11	19	[b]
Bronnitsky-2	56.36	68.89	3.2	13	38	[b]
Voronezh	55.73	[d]	5.5	10	19	[b]
Trostianets	53.91	79.79	6.4	9	15	[b]
Chita	54.26	106.06	-3.1	13	17	[c]

[a] Iroshnikov, 1977, omitting High Sayan (poor survival and growth)
[b] Tables 1-4, NEED REFERENCE
[c] Milyutin, NEED REFERENCE
[d] longitude not known

Table 3. Planting sites supplying independent data for judging the effectiveness of procedures for adjusting pine heights to a common age. The regression coefficient of adjusted height on observed.

planting site		age height adjusted to	age height adjusted from	number of observations	mean error (cm)	mean height (cm)	error (%)	regression coefficient
location	mean annual temperature							
Maine								
Crawford	5.4	11	13	48	27	394	6	1.05**
Smith Creek	3.5	11	13	46	25	298	8	1.07**
Ragmuff	3.5	11	13	36	19	277	7	1.08**
Minnesota	3.7	11	15	34	25	331	7	1.21**
Alberta								
Blue Ridge	1.3	13	14	47	-6	211	3	0.98†
Footner Lake	-2.3	13	16	25	-28	271	10	0.96†
Smoky Lake	1.5	13	16	25	38	408	9	1.17**
Duck Lake	1.2	13	20	66	122	476	26	1.22**

**significantly different ($P < 0.01$) from 1.0
† not significantly different from 1.0
note: intercepts differed significantly from zero for analyses of data from Smoky Lake ($P < 0.01$), Minnesota ($P > 0.03$), and Duck Lake ($P < 0.01$).

Table 4. Planting sites supplying independent data for judging the effectiveness of procedures for adjusting larch heights to a common age. The regression coefficient is of adjusted height on observed. Bronnitsky is listed in Table 2 with Footner Lake in Table 3.

planting site	age height adjusted to	age height adjusted from	number of observations	mean error (cm)	mean height (cm)	error (%)	regression coefficient
Bronnitsky-1	11	10	18	18	458	4	1.04†
Footner Lake	15	7	28	-18	431	4	0.95†

† not significantly different from 1.0
note: intercepts did not differ significantly from zero

Table 5. Results of regression analyses for predicting height and survival of *Pinus sylvestris* populations from climate transfer and provenance climate.

climate transfer variable	number of observations	Simple correlation of predicted with observed		provenance climate variable in combined model
		Weibull model	combined response model	
height at 11 years				
moisture index	1563	0.22**	0.41**	degree-days>5
continentality index	1632	0.44**	0.55**	degree-days>5
degree-days<0	1625	0.41**	0.54**	degree-days>5
degree-days>5	1554	0.21**	0.48**	degree-days>5
mean annual temperature	1626	0.33**	0.52**	degree-days>5
Survival				
Moisture index	369	0.44**	0.54**	degree-days>5
Continentality index	365	0.50**	0.53**	degree-days>5
Degree-days<0	371	0.64**	0.65**	degree-days>5
Degree-days>5	371	0.07ns	0.16**	degree-days>5
Mean annual temperature	383	0.58**	0.59**	moisture index

** statistically significant at $P < 0.01$
ns not significant

Table 6. Results of regression analyses for predicting height and survival of populations of *Larix* spp. from climate transfer and provenance climate.

climate transfer variable	number of observations	simple correlation of predicted with observed		provenance climate variable in combined model
		Weibull model	Combined response model	
height at 11 years				
moisture index	222	0.43**	0.42**	mean annual
continentality index	216	0.31**	0.39**	mean annual
degree-days<0	222	0.38**	0.44**	mean annual
degree-days>5	222	0.44**	0.49**	mean annual
mean annual temperature	225	0.43**	0.50**	mean annual
survival				
moisture index	172	0.53**	0.61**	moisture index
continentality index	171	0.24**	0.31**	moisture index
degree-days<0	172	0.28**	0.33**	moisture index
degree-days>5	172	0.31**	0.32**	moisture index
mean annual temperature	175	0.30**	0.35**	moisture index

** statistically significant at $P < 0.01$
ns not significant

Table 7. Simple correlations of heights predicted by the Weibull and combined response models with *Pinus sylvestris* data independent of the modeling procedures. Correlations are based on 313 observations.

climate transfer variable	simple correlations of predicted with observed	
	Weibull model	combined response model
moisture index	0.46**	0.45**
continentality index	0.26**	0.53**
degree-days<0	0.22**	0.44**
degree-days>5	0.09ns	0.61**
mean annual temperature	0.16**	0.48**

** statistically significant at $P < 0.01$
ns not significant

Table 8. Simple correlations of heights predicted by the Weibull and combined response models with *Larix* spp. data independent of the modeling procedures. Correlations are based on 21 observations.

climate transfer variable	simple correlations of predicted with observed	
	Weibull model	combined response model
moisture index	0.65**	0.73**
continentality index	0.45*	0.68**
degree-days<0	0.73**	0.73**
degree-days>5	0.28ns	0.80**
mean annual temperature	0.52**	0.68**

** statistically significant at $P < 0.01$
* statistically significant at $0.05 > P > 0.01$
ns not significant

Table 9. Statistics useful for ecological interpretation of the Weibull functions for *Pinus sylvestris*. Bold face type denotes intervals of climate change that do not include zero. Values of X and Y refer to x- and y-axis coordinates, respectively. X_1 and X_2 are the x-axis coordinates (smallest and largest, respectively) of the points of intersection of the Weibull function with the lower confidence interval ($a = 0.2$) of Y_{max}.

climate transfer variable	value (cm) of Y at the apogee (Y_{max})	X–axis coordinate[a] of Y_{max}	X_1	X_2	interval size ($X_2 - X_1$)
height at 11 years					
moisture index	251	-0.36	-1.08	0.48	1.56
continentality index	264	1.52	-3.92	5.60	9.52
degree-days<0	261	171	-217	462	679
degree-days>5	259	436	**184**	**646**	**830**
mean annual temperature	258	1.45	-0.30	2.85	3.15
survival					
moisture index	0.74	0.00	-0.60	0.60	1.20
continentality index	0.77	-9.36	**-17.52**	**-2.56**	**14.96**
degree-days<0	0.79	656	**171**	**1044**	**873**
degree-days>5	0.74	142	-26	310	336
mean annual temperature	0.79	2.15	**0.75**	**3.20**	**2.45**

[a]Units for x-axis coordinates are °C except for the moisture index which is degree-days>5 per mm annual precipitation.

Table 10. Statistics useful for ecological interpretation of the Weibull height functions for *Larix* spp. Bold face type denotes intervals of climate change that do not include zero. Values of X and Y refer to x- and y-axis coordinates, respectively. X_1 and X_2 are the x-axis coordinates (smallest and largest, respectively) of the points of intersection of the Weibull function with the lower confidence interval ($a = 0.2$) of Y_{max}.

climate transfer variable	value (cm) of Y at the apogee (Y_{max})	X–axis coordinate[a] of Y_{max}	X_1	X_2	interval size ($X_2 - X_1$)
L. sukaczewii					
moisture index	512	0.09	-0.75	0.94	1.69
continentality index	516	-6.20	-17.0	3.4	20.4
degree-days<0	522	140	-596	784	1380
degree-days>5	525	166	-106	438	544
mean annual temperature	533	1.08	-1.48	3.32	4.80
L. sibirica					
moisture index	360	-0.02	-1.07	0.94	2.10
continentality index	344	-8.70	-29.5	10.8	40.3
degree-days<0	366	1152	**140**	**2164**	**2024**
degree-days>5	383	447	**150**	**711**	**561**
mean annual temperature	389	5.24	**2.36**	**8.12**	**5.76**
L. gmelinii					
moisture index	435	0.62	-0.44	1.68	2.12
continentality index	411	-8.75	-26.25	8.75	35.00
degree-days<0	422	784	-320	1888	2208
degree-days>5	393	98	-378	574	952
mean annual temperature	405	3.08	-1.48	7.16	8.64

[a]Units for x-axis coordinates are °C except for the moisture index which is degree-days>5 per mm annual precipitation.

Table 11. Statistics useful for ecological interpretation of the Weibull survival functions for *Larix* spp. Bold face type denotes intervals of climate change that do not include zero. Values of X and Y refer to x- and y-axis coordinates, respectively. X_1 and X_2 are the x-axis coordinates (smallest and largest, respectively) of the points of intersection of the Weibull function with the lower confidence interval ($\alpha = 0.2$) of Y_{max}.

climate transfer variable	value (cm) of Y at the apogee (Y_{max})	X–axis coordinate[a] of Y_{max}	X_1	X_2	interval size ($X_2 - X_1$)
L. sukaczewii					
moisture index	0.43	0.73	**-0.01**	**1.36**	**1.37**
continentality index	0.41	-0.20	-11.00	10.60	21.6
degree-days<0	0.50	416	**48**	**784**	**736**
degree-days>5	0.47	438	**166**	**642**	**476**
mean annual temperature	0.50	2.36	**0.76**	**3.96**	**3.20**
L. sibirica					
moisture index	0.44	1.04	**0.51**	**1.47**	**0.96**
continentality index	0.31	-2.20	-21.70	17.30	39.0
degree-days<0	0.31	600	-872	1980	2852
degree-days>5	0.33	447	**18**	**843**	**825**
mean annual temperature	0.33	5.24	**0.76**	**9.08**	**8.32**
L. gmelinii					
moisture index	0.33	1.04	**0.09**	**1.79**	**1.70**
continentality index	0.24	-23.75	**-42.5**	**-7.5**	**35.0**
degree-days<0	0.27	1888	**876**	**2808**	**1932**
degree-days>5	0.26	404	-174	914	1088
mean annual temperature	0.26	6.84	**2.36**	**11.00**	**8.64**

[a]Units for x-axis coordinates are °C except for the moisture index which is degree-days>5 per mm annual precipitation.

Captions for Figures

Figure 1. Fit of Weibull regression model to observed height (dots) of *Pinus sylvestris* populations in relation to the change in continentally index between the planting site and the provenance. Asterisks mark the dummy variables located in climates where pine does not survive.

Figure 2. Fit of Weibull regression model to observed survival (dots) of *Pinus sylvestris* populations in relation to the change in degree-days<0 between the planting site and the provenance. Asterisks mark the dummy variables located in climates where pine does not survive.

Figure 3. Fit of Weibull regression model to observed survival of populations of *Larix* spp. in relation to change in mean annual temperature between the planting site and the provenance. Asterisks mark the dummy variables located in climates where pine does not survive.

Figure 4. Fit of Weibull regression model to observed survival of populations of *Pinus sylvestris*. in relation to change in the moisture index between the planting site and the provenance. Asterisks mark the dummy variables located in climates where pine does not survive.

Figure 5. Combined response model for predicting the height of populations of *Pinus sylvestris* from the Weibull regression model driven by the change in the continentally index and from the number of degree-days>5 of the provenance.

Figure 6. Combined response model for predicting the survival of populations of *Pinus sylvestris* from the Weibull regression model driven by the change in degree-days<0 index and from the number of degree-days>5 of the provenance.

Figure 7. Combined response model for predicting the height of *Larix sukaczewii* (top), *L. sibirica* (center), and *L. gmelinii* (bottom) from the Weibull regression model driven by the change in mean annual temperature and from the mean annual temperature of the provenance.

Figure 8. Combined response model for predicting the survival *Larix sukaczewii* (top), *L. sibirica* (center), and *L. gmelinii* (bottom) from the Weibull regression model driven by the change in the moisture index and from the moisture index of the provenance.

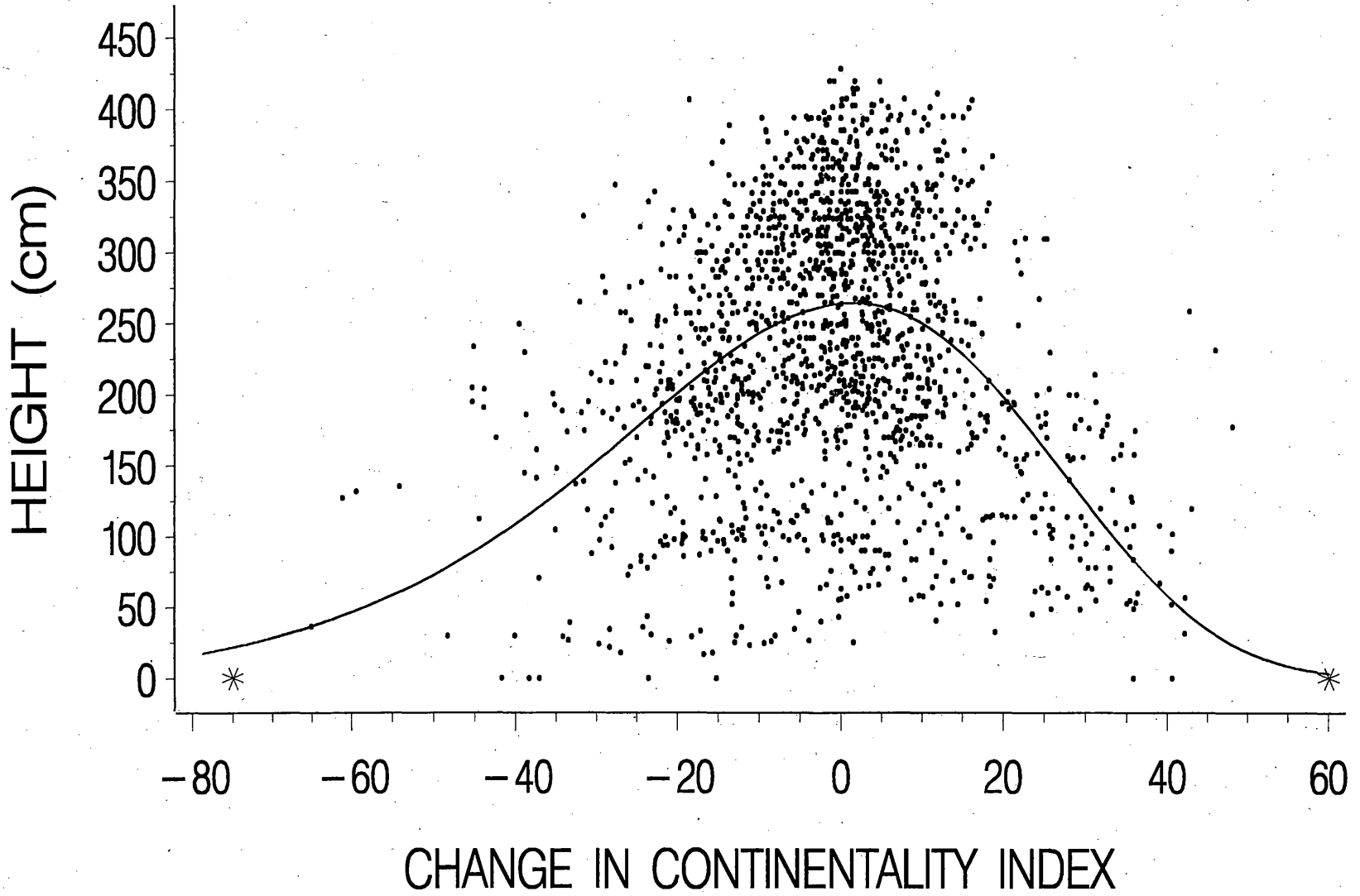

HEIGHT (cm)
450
400
350
300
250
200
150
100
50
0
−80
−60
−40
−20
0
20
40
60
CHANGE IN CONTINENTALITY INDEX

Figure 1

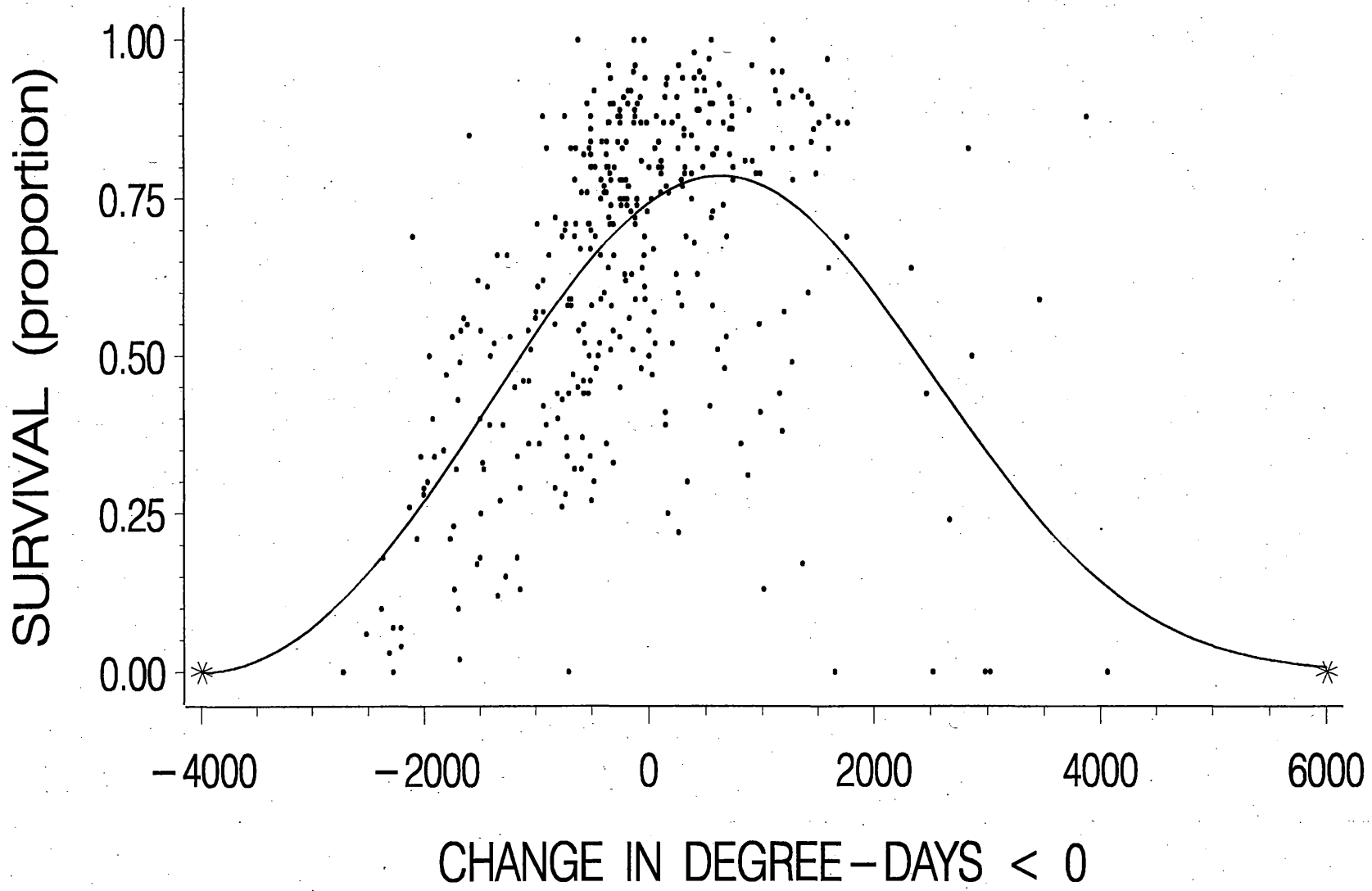

SURVIVAL (proportion)
1.00
0.75
0.50
0.25
0.00
−4000
−2000
0
2000
4000
6000
CHANGE IN DEGREE−DAYS < 0

Figure 2

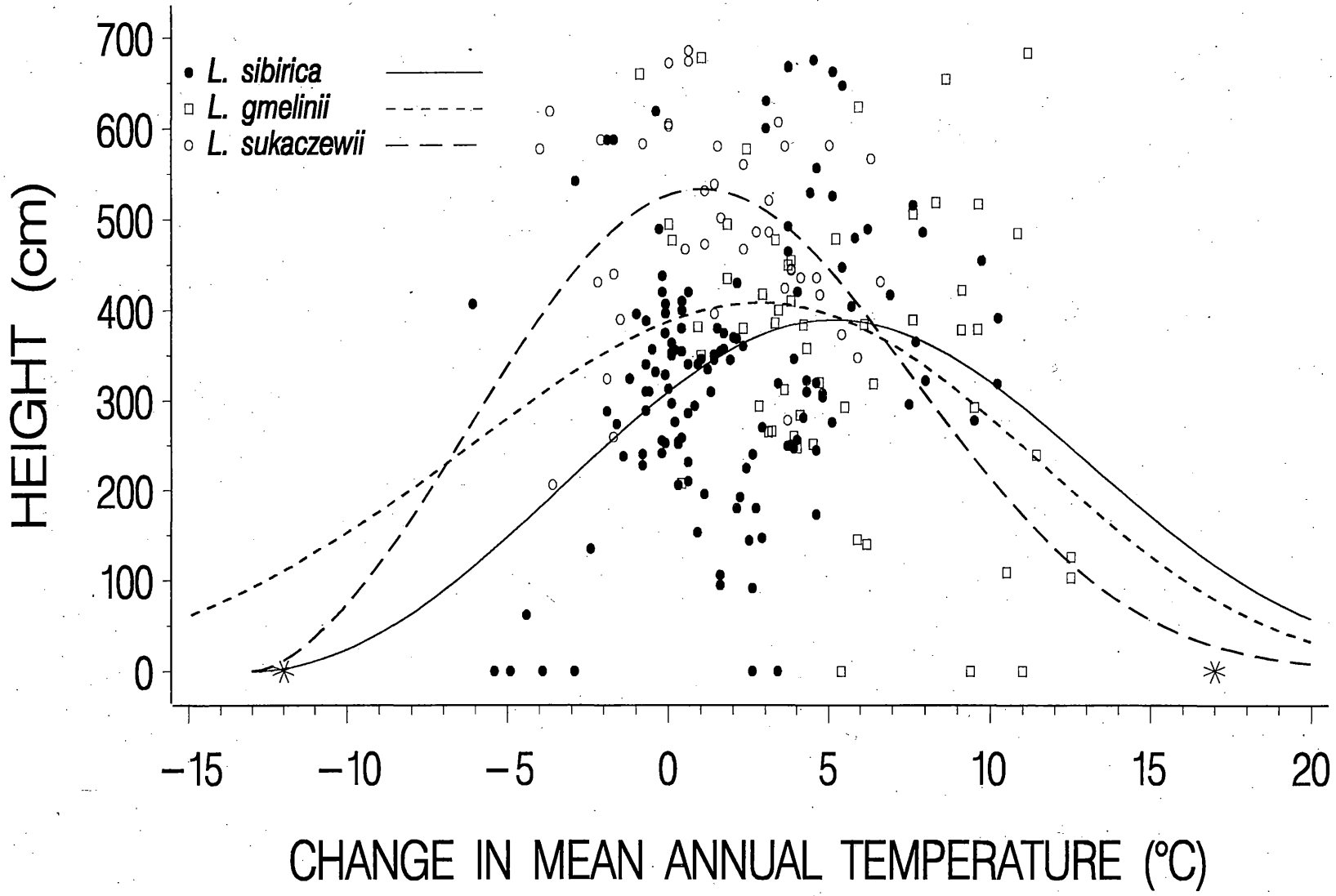

L. sibirica
L. gmelinii
L. sukaczewii
HEIGHT (cm)
700
600
500
400
300
200
100
0
−15
−10
−5
0
5
10
15
20
CHANGE IN MEAN ANNUAL TEMPERATURE (°C)

Figure 3

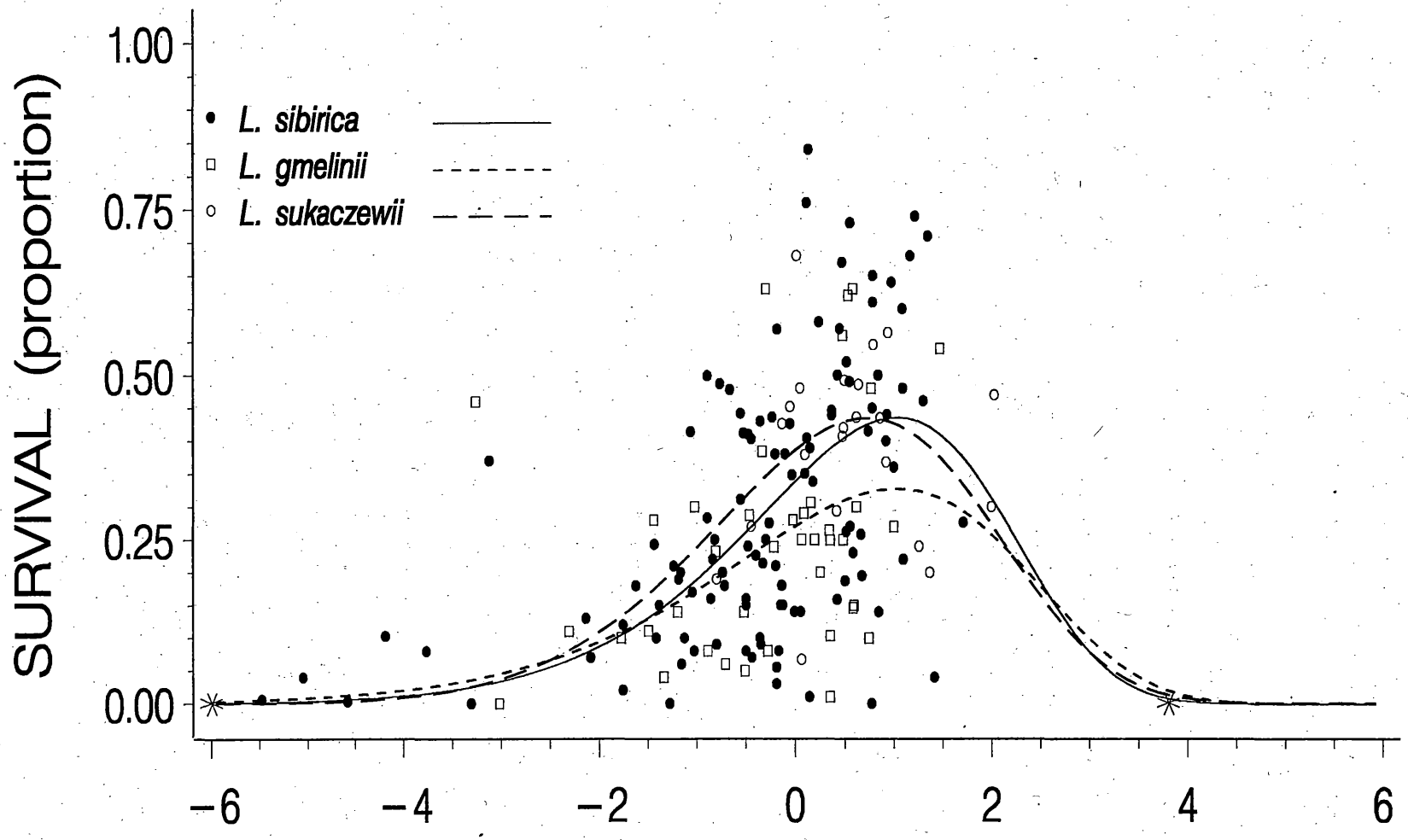

1.00
0.75
0.50
0.25
0.00
SURVIVAL (proportion)
L. sibirica
L. gmelinii
L. sukaczewii
−6
−4
−2
0
2
4
6
CHANGE IN MOISTURE INDEX

Figure 4

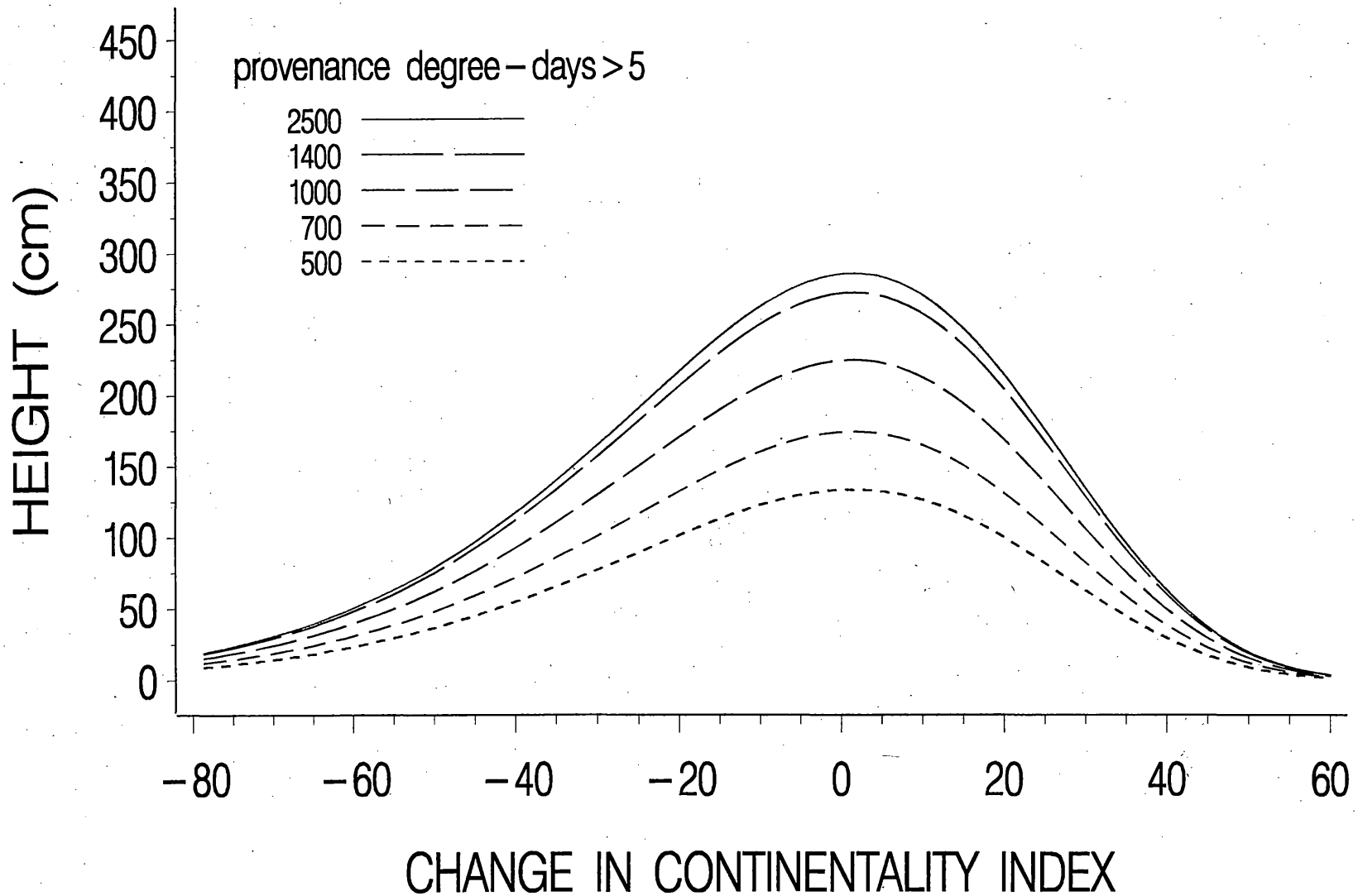

provenance degree – days > 5
2500
1400
1000
700
500
HEIGHT (cm)
450
400
350
300
250
200
150
100
50
0
−80
−60
−40
−20
0
20
40
60
CHANGE IN CONTINENTALITY INDEX

Figure 5

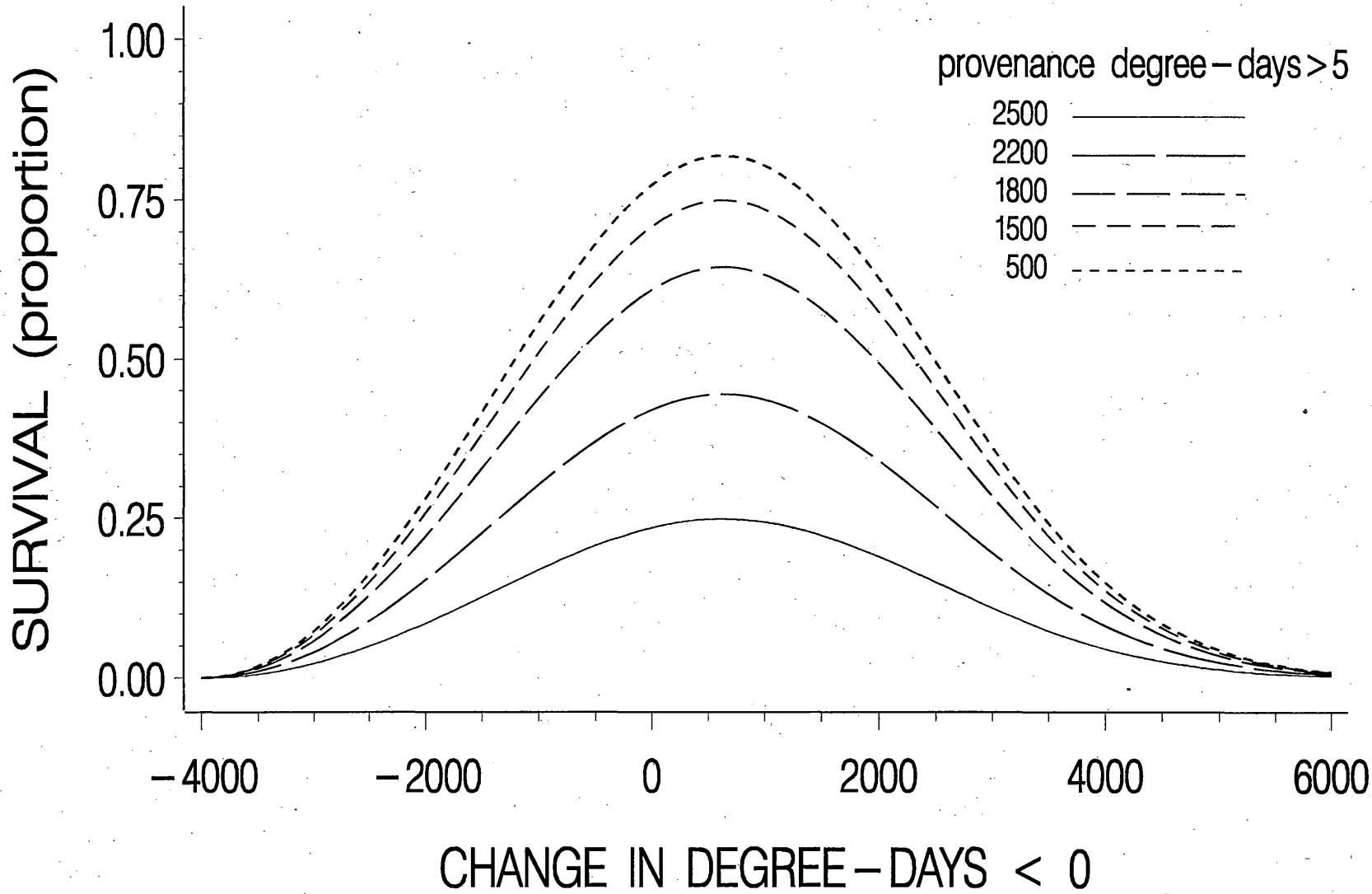
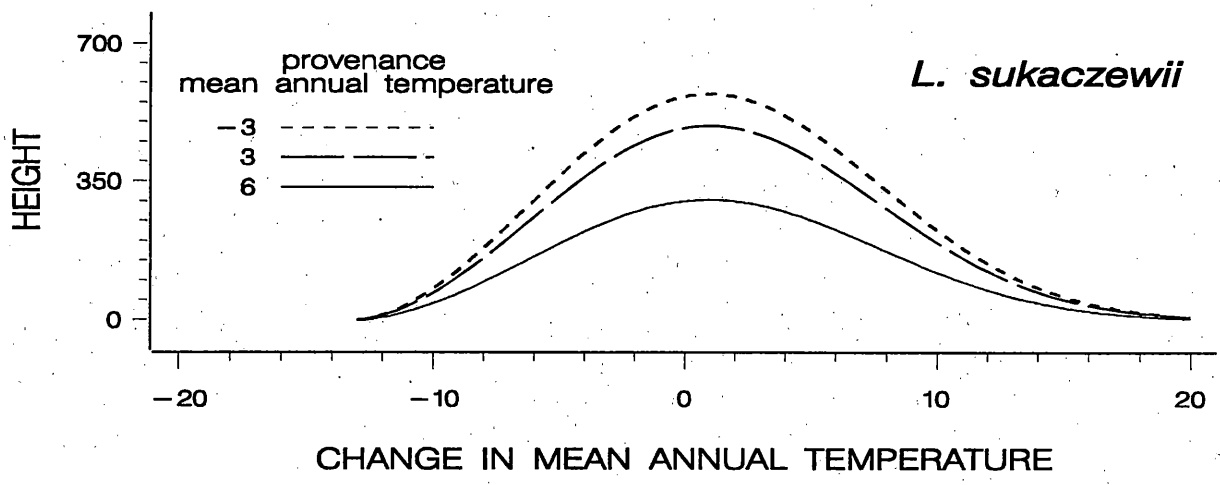
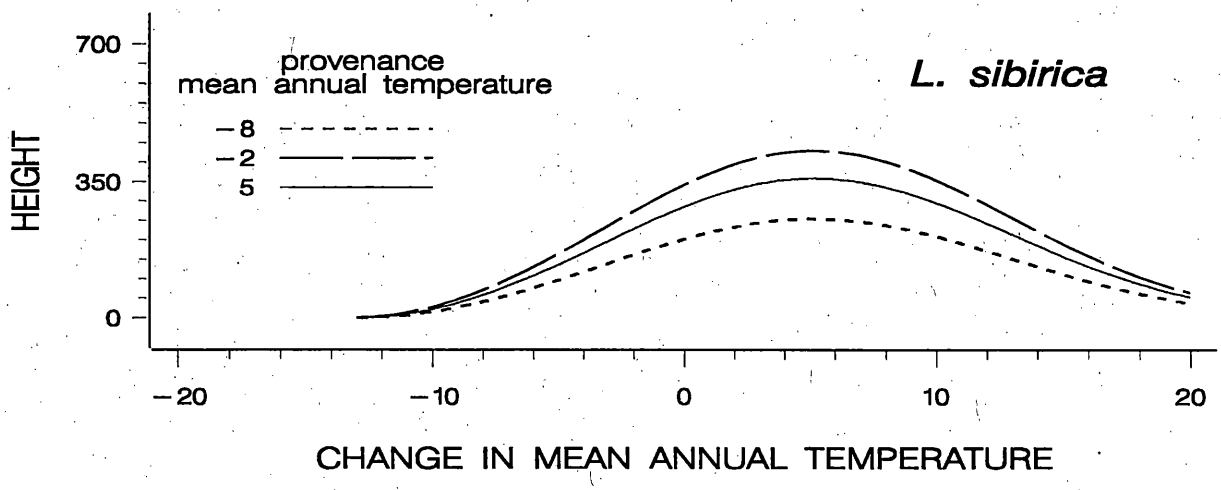

SURVIVAL (proportion)
1.00
0.75
0.50
0.25
0.00
provenance degree-days>5
2500
2200
1800
1500
500
-4000
-2000
0
2000
4000
6000
CHANGE IN DEGREE-DAYS < 0

Figure 6


700
350
0
HEIGHT
provenance
mean annual temperature
−3
3
6
L. sukaczewii
−20
−10
0
10
20
CHANGE IN MEAN ANNUAL TEMPERATURE


700
350
0
HEIGHT
provenance
mean annual temperature
−8
−2
5
L. sibirica
−20
−10
0
10
20
CHANGE IN MEAN ANNUAL TEMPERATURE

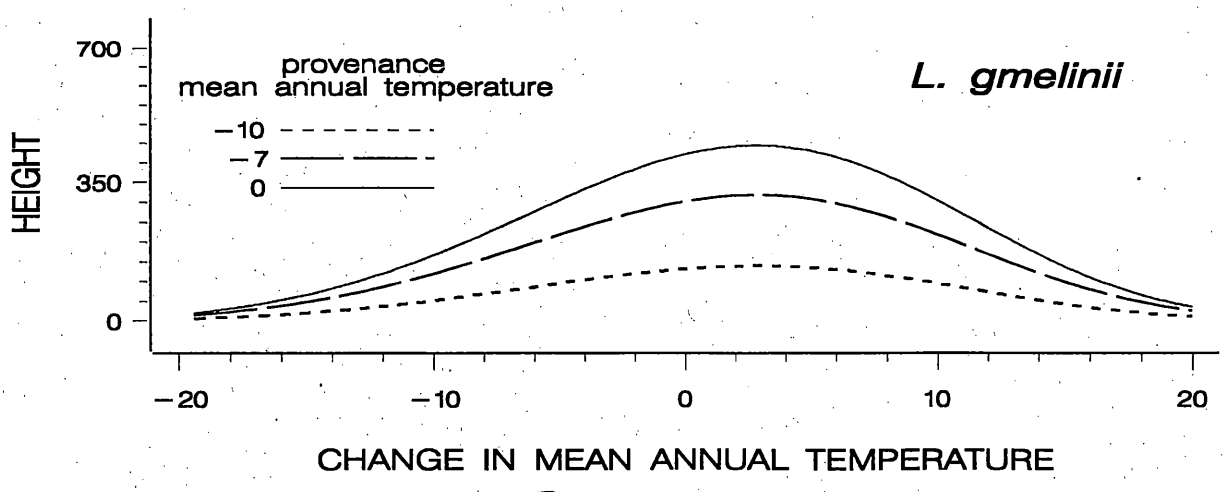
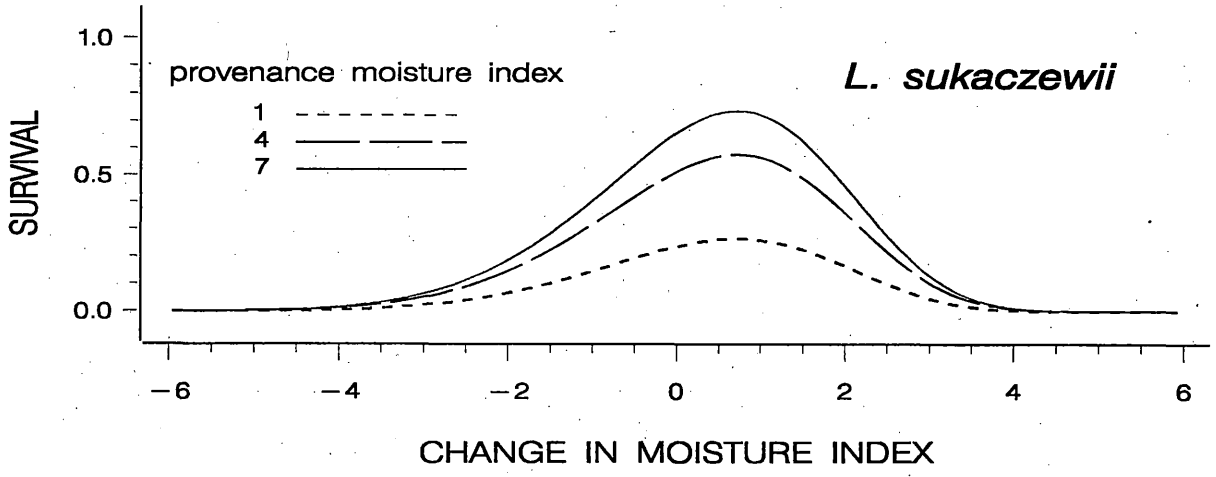
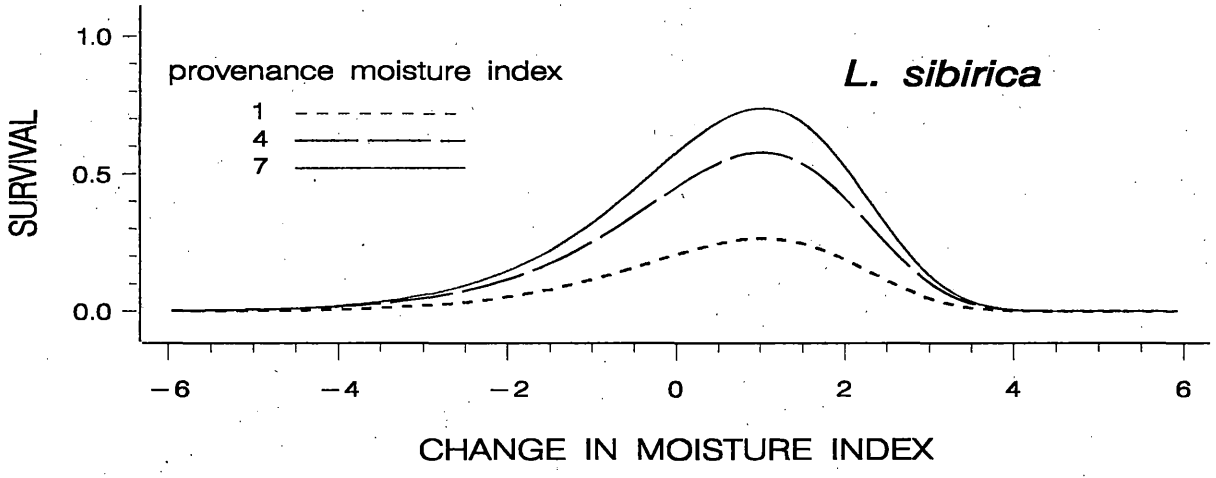

700
350
0
HEIGHT
provenance
mean annual temperature
−10
−7
0
L. gmelinii
−20
−10
0
10
20
CHANGE IN MEAN ANNUAL TEMPERATURE

Figure 7


1.0
0.5
0.0
SURVIVAL
provenance moisture index
1
4
7
L. sukaczewii
−6
−4
−2
0
2
4
6
CHANGE IN MOISTURE INDEX


1.0
0.5
0.0
SURVIVAL
provenance moisture index
1
4
7
L. sibirica
−6
−4
−2
0
2
4
6
CHANGE IN MOISTURE INDEX

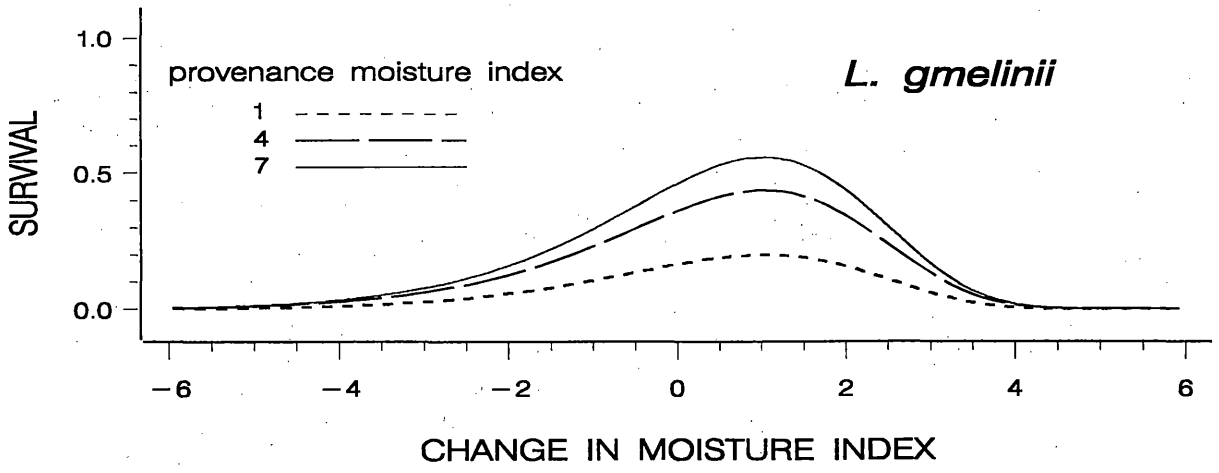

1.0
0.5
0.0
SURVIVAL
provenance moisture index
1
4
7
L. gmelinii
−6
−4
−2
0
2
4
6
CHANGE IN MOISTURE INDEX

Figure 8